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PLANT BUGS (HETEROPTERA: MIRIDAE) OF *PHLOX SUBULATA* AND OTHER NARROW-LEAVED PHLOXES IN EASTERN UNITED STATES

A. G. Wheeler, Jr.

Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg, Pennsylvania 17110.

Abstract.—*Phlox subulata* L. (Polemoniaceae) is a prostrate, suffruticose perennial characteristic of shale and serpentine barrens of the eastern United States. It serves as a host of various little-known insect species. The mirid fauna of this plant was inventoried during 1989–1994, mainly in shale barrens of Maryland, Pennsylvania, Virginia, and West Virginia, but also in outcrops of shale and other types of bedrock, and in eastern serpentine barrens. Four plant bug species were consistently collected in shale barrens: the bivoltine generalists *Lopidea heidemanni* Knight and *L. minor* Knight and the univoltine specialists *Polymerus tinctipes* Knight and *P. wheeleri* Henry; previously, the two monophagous species of *Polymerus* had been known only from their type localities in Maryland and West Virginia, respectively. Information on distribution, seasonal history, and habits is presented for all four species, as well as their use of the only other eastern narrow-leaved phloxes of prostrate growth habit, *P. bifida* and *P. nivalis*. *Lopidea minor, P. tinctipes,* and *P. wheeleri* are as characteristic of shale barrens as are the endemic plant species; these specialized communities and their associated biota are deserving of protection from habitat degradation.

Key Words: Insecta, Miridae, shale barrens, serpentine barrens, insect distribution, life history, host-plant specificity

Scientific interest in shale barrens is generally restricted to botanists and geologists.
—R. B. Platt 1951

Geologists and botanists are agreed that outcrops of Devonian shales may be traced by the presence on them of creeping phlox (*Phlox subulata*) . . .
—M. Brooks 1965

Shale barrens of the mid-Appalachian region—extending from south-central Pennsylvania (40°N) through western Maryland to eastern West Virginia and southwestern Virginia (37°N)—have long fascinated field botanists (Wherry 1930, Platt 1951). The barrens occur on discontinuous shale outcrops and talus of steep southern exposure (>20°) that are characterized by high insolation temperatures and low moisture availability at the surface; they are often undercut by a stream. Shale barrens, in the lee of mountains and within rain shadows, receive an average rainfall of 70 to 100 cm per year (Platt 1951, Brooks 1965, Keener 1983, DeSelm and Murdock 1993). Despite the hot, dry microclimate and sparse vegetation—treeless openings are common—these shale slopes retain sufficient soil moisture to sustain the growth of herbaceous endemic plants (Platt 1951, Keener 1983).

Occurring mainly on Upper Devonian

shales of the Brallier formation, shale barrens may also be associated with Ordovician Martinsburg shales or even Silurian strata (Artz 1937, Platt 1951, Keener 1983, Morse 1983). Like other unusual soil types, these edaphic islands in the eastern deciduous forest of the Valley and Ridge phytogeographic province (Appalachian Valley) support a distinctive flora (e.g., Wherry 1930, Core 1940, 1952, Allard and Leonard 1946, Platt 1951, Henry 1954, Keener 1970, 1983, Morse 1993). The presence of several endemic plants, disjuncts, and various rare or endangered plant taxa that are absent or seldom present in the surrounding woodlands suggests the occurrence of a diverse fauna of phytophagous insects. Such is indeed the case (A.G.W. unpublished data), although entomologists have paid relatively little attention to insect-plant relationships in these communities. The butterflies and skippers characteristic of shale barrens, however, are well known (Clench and Opler 1983, Opler and Krizek 1984, Pague and Schweitzer 1991), and Pennsylvania shale barrens contain some of that state's rarest butterfly and moth species (Smith 1989). Species in a few other insect groups have also been studied, e.g. the grasshopper *Melanoplus impudicus* Scudder (Gurney 1941) and the psyllid *Craspedolepta eas* (McAtee) (Wheeler 1994).

Moss phlox, or moss or mountain pink (*Phlox subulata* L.), is a prostrate or matlike suffruticose (i.e. becoming somewhat woody) perennial that characterizes shale barrens. It harbors an unusually rich insect fauna, including the recently described whitefly *Trialeurodes phlogis* Russell (Russell 1993), and several other poorly known species (Henry 1979, Wheeler et al. 1983, Wheeler 1994, unpublished data). In the present paper, I provide biological information on the mirids or plant bugs that develop on *P. subulata* growing on various types of bedrock; mirid-moss phlox relationships in mid-Appalachian shale barrens are emphasized. Data from an inventory of the mirids associated with other eastern subulate or narrow-leaved phloxes are also presented. This paper commemorates the remarkably productive scientific career of José C. M. Carvalho and his devotion to the Miridae. His research and numerous publications, including a world catalog of the group, stimulated interest in mirid systematics and biology.

Host Plants

The genus *Phlox* belongs to the Polemoniaceae, a mostly New World family. It contains numerous endemic eastern species but is most diverse in western North America (Grant 1959). Mirids were collected principally from *P. subulata,* although collections were also made from *P. bifida* Beck and *P. nivalis* Lodd. ex Sweet. These three apparently closely related species (particularly *P. bifida* and *P. subulata* [Gleason and Cronquist 1964]) are the only narrow-leaved members of the genus (Section or Subsection Subulatae) occurring in eastern North America (Wherry 1935b, 1951, Flory 1970). *Phlox nivalis* is sometimes relegated to the Section Protophlox (Wherry 1955) but is actually similar in both morphology and cytology to *P. bifida* and *P. subulata* (Smith and Levin 1967).

Phlox subulata.—Moss phlox (Figs. 1, 2) is a suffruticose perennial that has many-branched trailing or creeping stems, is woody at the base, and has persistent awl-shaped or needlelike leaves. The main blooming period is April to May, or in cooler localities, into June; colonies vary in flower color from rose-purple to pink or white. Forming dense, low, evergreen mats on sandy or gravelly soil and rocky ledges (Fig. 1), moss phlox occurs not only in shale barrens but also in serpentine barrens, on limestone cliffs, and on other types of bedrock (Stout 1917, Wherry 1929a, 1930, 1936, 1955, 1964, Core 1966, Everett 1981, Keener 1983, Bartgis 1985). *Phlox subulata* typically grows in well-drained, slightly alkaline to strongly acidic soils. This pioneer, xero-

Figs. 1–2. *Phlox subulata.* 1, Colony on shale outcrop in West Virginia. 2, Close-up of inflorescence. (Photographs courtesy of T. J. Allen.)

phytic plant is seldom found in nearby woods or meadows, where it is outcompeted by faster-growing plants (Wherry 1929b, 1935b, Allard and Leonard 1946, Morse 1988).

Moss phlox is native from southern Ontario and New York to southern Michigan and south to the mountains of North Carolina and Tennessee (Wherry 1929b, 1935b, 1955, Flory 1970, Everett 1981, Gleason and Cronquist 1991). Its dispersal center may be the Appalachians of eastern West Virginia (Wherry 1935b). *Phlox subulata* is used extensively in rock gardens and borders, and as a ground cover on slopes; it often escapes from cultivation, establishing colonies in cemeteries and on artificial barrens such as road and railroad cuts (Wherry 1929b, c, Everett 1981, Cooperrider 1986, Hudak 1993).

Phlox bifida.—Cleft or sand phlox is a tuft-forming species superficially similar to *P. subulata.* It differs, however, in its looser, often more erect, growth habit; longer leaves, which are fewer in number; and deeply cleft (bifid) petal blades. Flowers vary from pale blue or violet to white, but are mostly lavender. This spring-blooming perennial shows a disjunct distribution from southern Michigan to Tennessee, northern Arkansas, and eastern Kansas. A plant mainly of the Interior Highland and Low Plateaus with its range centering in southern Illinois, this pioneer species colonizes sandy banks and dunes, rocky slopes, and bare cliffs (Wherry 1929b, 1935b, 1955, Winterringer and Vestal 1956, Everett 1981, Gleason and Cronquist 1991).

Phlox nivalis.—Piney-woods or trailing phlox has foliage similar to that of *P. subulata,* but some of its leaves are usually broader. Although these species have been confused botanically, they differ markedly in floral structure: *P. nivalis* has much shorter stamens and style and somewhat larger flowers. The specific epithet, *nivalis,* refers to the often snowy white flowers, but the corolla may be pink or light purple. More southern in distribution than the other eastern narrow-leaved phloxes, *P. nivalis* ranges from southern Virginia to Florida and Alabama. Its dispersal center lies in the Piedmont of South Carolina. Piney-woods phlox grows mainly in acid soils on dry sandy slopes of open pine and oak woods. It blooms from March to April in the southern part of its range, April and May toward the northern end (Wherry 1929b, 1935b,d, 1955, Everett 1981, Gleason and Cronquist 1991).

Study Sites and Methods

Mirids were observed and collected from 1989 to 1994, chiefly on *P. subulata* in mid-Appalachian shale barrens of Upper Devonian strata and Ordovician Martinsburg outcrops (Fig. 3). Included were such well-known botanical sites as Green Ridge in Maryland; Eagle Rock, Head Waters, Millboro, and Short Mountain in Virginia; and Kates Mountain in West Virginia (Wherry 1935a, Butts 1940, Core 1940, 1952, Allard and Leonard 1946, Platt 1951, Keener 1983, Morse 1983). Numerous shale outcrops that cannot be characterized as true barrens were also sampled in the Valley and Ridge Province, as were a few ornamental plantings. In addition, collection sites included eastern serpentine barrens such as Nottingham, Pink Hill, and Unionville in Pennsylvania, and Soldiers Delight in Maryland (Wheeler 1988 and references therein), and sites in the Appalachian Highlands where *P. subulata* grows on dolomite, greenstone, limestone, and other substrates. Limited sampling was conducted to determine the mirid fauna of *P. subulata* outside this plant's center of distribution: in Kentucky, New Jersey, New York, North Carolina, and Ohio. Information on seasonality and habits of mirids associated with *P.subulata* was obtained largely from the following sites; the number of visits to each site is given in parentheses (see also Table 1).

MARYLAND: *Allegany Co.*, Country Club shale barren above Evitts Cr., NE. of Cumberland (3) and shale barrens, Green Ridge State Forest, Fifteen Mile Creek Rd.

Table 1. Miridae observed on *Phlox subulata* during 1989-1994; asterisks denote ornamental plantings.

State	County	Locality	*Lopidea heidemanni*	*L. minor*	*Polymerus tinctipes*	*P. wheeleri*
Maryland	Allegany	Country Club shale barren, NE. of Cumberland	●			●
		Fort Hill, south tip ridgetop			●	
		Green Ridge State Forest, Fifteen Mile Creek Rd. at Piclic Rd.	●		●	
		Romney-Oldtown shale barren, E. of Oldtown	●		●	
	Baltimore	Soldiers Delight serpentine barren, SW. of Reisterstown	●	●		
	Montgomery	Great Falls			●	
	Washington	Boy Scout shale barren, Sideling Hill Wildlife Management Area	●	●	●	
North Carolina	Union	*N. of Fairview, Rt. 601	●			
Ohio	Athens	Buffalo Beats prairie, SE. of Buchtel			●	
		York Twp., Twp. Rd. 73, 0.3 mi. W. of Co. Rd. 1	●		●	
		York Twp., Twp. Rd. 293 nr. junc. Twp. Rd. 295	●		●	
	Guernsey	N. of Winterset, Twp. Rd. 871	●		●	
Pennsylvania	Allegheny	SW. of Tarentum, Bull Creek Rd.	●			
	Bedford	E. of Fishertown, Rt. 56	●		●	
		NE. of Ryot, Rt. 96	●		●	●
		Silver Mills shale barren, E. of Inglesmith	●		●	
	Chester	Fern Hill serpentine barren, West Goshen Twp.	●			
		Nottingham Park serpentine barren	●	●		
		Sugartown serpentine barren, Willistown Twp.	●	●		
		Unionville serpentine barren, NE. of Unionville	●	●		
	Delaware	Pink Hill serpentine barren, Tyler Arboretum, nr. Lima	●		●	
	Monroe	NE. of Shawnee, Mosier Knob Rd.	●	●		
	Northumberland	*2 mi. E. of Milton, Rt. 642			●	
Virginia	Alleghany	7.6 mi. S. of Covington, Rt. 18	●			
		10.6 mi. S. of Covington, Rt. 18	●	●	●	
		N. of Sweet Chalybeate, Rt. 311	●			
	Bath	Fort Lewis shale barren, Rt. 678 at Cowpasture River	●	●	●	
		3 mi. SW. of Millboro Springs, Rt. 42	●	●		
		*Millboro			●	
	Bland	3.5 mi. SW. of Bland, Rt. 42	●			
		1.2 mi. E. of Crandon, Rt. 42	●			
	Botetourt	Eagle Rock shale barren, 2.5 mi. NW. of Eagle Rock		●		
	Carroll	SE. of Dugspur, Rt. 638	●	●		
	Floyd	*SE. of Willis, Rt. 799	●	●		
	Highland	Head Waters shale barren	●	●		●
		E. of Frost, W. Va., Rt. 600 S. of Rt. 64	●			
	Madison	Shenandoah Nat. Park, Skyline Drive, Franklin Cliffs	●	●	●	
	Montgomery	Coffee Valley, S. of Ironto	●	●		
		N. of Ironto, Rt. 713	●		●	
	Page	Shenandoah Nat. Park, Skyline Drive, Little Stony Man Cliffs		●		
	Roanoke	Dixie Cliff, SW. of Glenvar	●	●	●	
		S. of Catawba, Rt. 311			●	
	Rockbridge	Goshen, Rts. 39-42	●		●	
	Rockingham	George Washington Nat. Forest, For. Rd. 87, W. of Fulks Run		●		
	Shenandoah	2.5 mi. N. of Edinburg, Rt. 675	●		●	
		Short Mountain shale barren, 3 mi. SE. of Mount Jackson	●	●	●	●

at Piclic Rd. (5); *Baltimore Co.*, serpentine barrens, Soldiers Delight Natural Environmental Area, W. of Owings Mills (3); *Washington Co.*, Boy Scout shale barren above Sideling Hill Cr., E. of Little Orleans (4).

OHIO: *Athens Co.*, Buffalo Beats prairie, SE. of Buchtel (2); *Guernsey Co.*, shale banks along county road, NW. of Winterset (3).

Table 1. Continued.

State	County	Locality	*Lopidea heidemanni*	*L. minor*	*Polymerus tinctipes*	*P. wheeleri*
West Virginia	Greenbrier	Kates Mountain shale barren, S. of White Sulphur Springs	●	●	●	
		White Sulphur Springs	●	●	●	
		E. of Alvon, Whites Draft Rd.	●	●	●	
	Grant	Cave Mountain, 1 mi. N. of Landes	●	●	●	
		N. of Arthur, Patterson Creek Rd.				●
		4 mi. N. of Landes, Rt. 220		●		
		2.3 mi. S. of Landes, Rt. 220	●			
		3 mi. S. of Landes, Rt. 220				●
		3.5 mi. S. of Petersburg, Rt. 220	●			
	Hampshire	S. of Romney, River Rd.	●	●		
		nr. Forks of Cacapon, Rt. 29,0.3 mi. S. of Rt. 127	●			
		3 mi. E. of Augusta, Rt. 50	●			
		Shanks, Rt. 50	●			●
		3 mi. E. of Romney, Rt. 50	●			
		8 mi. W. of Romney, Rt. 50	●			
		3.5 mi. N. of Slanesville, Rt. 29	●			●
		Mathias, Lost River Rd.	●			
		NW. of Lost River State Park, Lost River Rd.	●			
		Mooresfield, South Fork Rd.		●		
		N. of Mooresfield, Rt. 220	●	●	●	
		7.5 mi. NE. of Mooresfield, Trough Rd.	●			●
		2 mi. E. of Wardensville, Rt. 55		●	●	
	Mineral	Burlington, Rt. 50	●			●
	Morgan	Largent, Rt. 9	●			
		10 mi. S. of Great Cacapon, Rt. 9			●	
	Pendleton	nr. Fort Seybert, Conrad Rd.	●			
		North Fork Mountain, nr. Smoke Hole		●		
		2.3 mi. SE. of Upper Tract, Schmucker Rd.	●	●		●
		E. of Brandywine, Rt. 33		●		
		N. of Brandywine, Rt. 33	●	●		●
		6 mi. S. of Franklin, Rt. 220	●			
	Pocahontas	NW. of Huntersville, Rt. 28	●		●	
		3.5 mi. SE. of Minnehaha Springs, Rts. 39-92	●			

PENNSYLVANIA: *Bedford Co.*, roadside slope, NE. of Ryot (4); *Chester Co.*, Nottingham(3),Sugartown(4),andUnionville (2) serpentine barrens; *Delaware Co.*, Pink Hill serpentine barren, Tyler Arboretum, NE. of Lima (4); *Monroe Co.*, roadside bank along Mosier Knob Rd., NE. of Shawnee (2).

VIRGINA: *Alleghany Co.*, shale barren above Potts Creek, Rt. 18, 10.6 mi. SW. of Covington (8); *Bath Co.*, shale barren above Cowpasture River, Rt. 678, Ft. Lewis (5); *Highland Co.*, Head Waters shale barren above Shaws Fork, nr. junc. Rts. 250 and 616 (19); *Montgomery Co.*, shaly slope, Rt. 622 nr. junc. Rt. 603 N. of Ironto (5); *Roanoke Co.*, Dixie Cliff, SW. of Glenvar (2); *Rockbridge Co.*, shale slopes along Rts. 39–42, Goshen (9); *Rockingham Co.*, shaly banks along For. Rd. 87, George Washington National Forest, W. of Fulks Run (4); *Shenandoah Co.*, shale barren, south end of South Mountain, SE. of Mount Jackson (8).

WEST VIRGINIA: *Greenbrier Co.*, shale barren, Kates Mountain, S. of White Sulphur Springs (9) and shale banks along

Fig. 3. Occurrence of mid-Appalachian shale barrens based on Keener (1983); larger stippled area = Upper Devonian shale strata, smaller area = Ordovician Martinsburg outcrops in the Massanutten Mountains.

Whites Draft Rd., E. of Alvon (3); *Hampshire Co.*, roadside slopes, Rt. 29, 3.5 mi. N. of Slanesville (6) and Rt. 50, Shanks (6); *Hardy Co.*, shale banks along Lost River Rd., W. of Mathias (2); *Mineral Co.*, shale banks, Rt. 50 nr. Burlington (2), *Pendleton Co.*, shale banks along Schmucker Rd., SE. of Upper Tract (3).

Mirids were sampled on *P. bifida* in Illinois along bluff top woods, LaRue-Pine Hills Ecological Area, Shawnee National Forest, Union Co.; on limestone bluffs near Prairie du Rocher, Randolph Co.; and in Mason Co. in loess hill prairie, Revis Nature Preserve SW. of Mason City, and in sand prairie, Sand Ridge State Forest NE. of Havana. Collections were made in Indiana on limestone bluffs above the Ohio River at Porters Point, SW. of Laconia, Harrison Co.; in Kentucky on limestone ledges of "Boones Knoll," Camp Nelson, Jessamine Co.; and in Tennessee in cedar glades near Cedars of Lebanon State Park and at Long Hunter State Recreation Area, Wilson Co.

Limited sampling of mirids associated with *P. nivalis* was conducted. In North Carolina a collection was made from a roadside bank along Rt. 601 W. of Stanfield, Cabarrus Co.; no mirids were found on this plant at Bluff Mountain, N.C., or at several sites in South Carolina (Lexington, Pickens, and York counties).

The main collecting sites were visited at irregular intervals from early or mid-April through June; in some years, sampling of *P. subulata* began in late March and extended into early October. At each site, mirids were sampled by shaking mats of phlox over a shallow white tray and recording any mirid species present and their relative abundance. Sampling times varied from 10–15 minutes for small host patches to 45–60 minutes or more for sites having extensive phlox colonies. In the first season of study

(1989), different-appearing nymphs were reared on sprigs of the host plant to associate them with adults of the various mirids. Nymphal stages of each species present were recorded in the field or, when necessary, collected and sorted to instar in the laboratory. Information on feeding habits was obtained in the field and supplemented by laboratory observations. Voucher specimens of the four phlox-associated mirids have been deposited in the collections of Cornell University, Ithaca, N.Y.; the National Museum of Natural History, Washington, D.C.; and the Pennsylvania Department of Agriculture, Harrisburg.

Results

Information is presented on four mirid species that occur consistently on *P. subulata*: the generalists *Lopidea heidemanni* Knight and *L. minor* Knight (Orthotylinae: Orthotylini) and specialists *Polymerus tinctipes* Knight and *P. wheeleri* Henry (Mirinae: Mirini). For each species, the known distribution is summarized and any new state records obtained are noted; literature on host plants, including those used for reproduction as well as adult feeding, is reviewed; and the seasonal history and habits on *P. subulata* are summarized. Associations with other plants found in shale barrens and shale outcrops, and on other narrow-leaved eastern phloxes, are included. Nymphs of the phyline *Plagiognathus politus* Uhler occasionally developed on *P. subulata* in shale barrens, but this polyphagous species will not be mentioned further.

Lopidea heidemanni Knight

This polyphagous plant bug, common on weedy vegetation along roads and in other disturbed habitats, is more likely to be encountered by the general collector than the other phlox-associated mirids that were studied. Despite its wide range and frequency of collection, the habits of *L. heidemanni* are not well known.

Distribution.—Described by Knight (1917) from New York, *L. heidemanni* has since been recorded from 30 additional states and the District of Columbia, ranging from Vermont, south to Georgia, and west to Minnesota, Wyoming, and Texas (Henry and Wheeler 1988, Asquith 1991). Although *L. heidemanni* was present on *P. subulata* at 62 of 79 sites that yielded plant bugs (Table 1), no new state records were obtained during this study. Asquith (1991) mapped the known distribution of this species.

Host plants.—Nymphs have been recorded from yarrow (*Achillea millefolium* L.), ninebark (*Physocarpus opulifolius* (L.) Maxim.), and terminal growth of young elm (*Ulmus* sp.) (Knight 1923, 1941, Wheeler and Hoebeke 1985). This species has also been collected on numerous other herbs, shrubs, and trees (e.g. Messina 1978, Snodgrass et al. 1984, Blinn and Yonke 1985, Asquith 1991). Because adults readily disperse to various plants (see "Seasonal history and habits"), some of the recorded "hosts" may be used only for adult feeding or shelter. Although this species is said to develop mainly on deciduous trees (Asquith 1993), herbs would appear to be used more frequently as host plants than shrubs or trees.

In the present study, nymphs developed on *Phlox bifida* and *P. nivalis,* and on *P. subulata* in native colonies and landscape plantings. In shale barrens and outcrops, nymphs were also observed on *Ceanothus americanus* L., *Centaurea biebersteinii* DC. (= *C. maculosa* of authors), *Clematis albicoma* Wherry, *Crataegus* sp., *Draba ramosissima* Desv., *Eriogonum allenii* S. Wats., *Oxalis stricta* L., *Penstemon canescens* (Britt.) Britt., *Rhus aromatica* Ait., *Senecio antennariifolius* (Britt.) Britt., *Silene caroliniana* ssp. *pensylvanica* (Michx.) Clausen, *Thlaspi perfoliatum* L., and *Vicia villosa* Roth. Adults were found on *Hypericum prolificum* L., *Quercus ilicifolia* Wangenh., *Rhus copallinum* L., and *Senecio anonymus* Wood in shale barrens. A common breeding host in serpentine barrens was

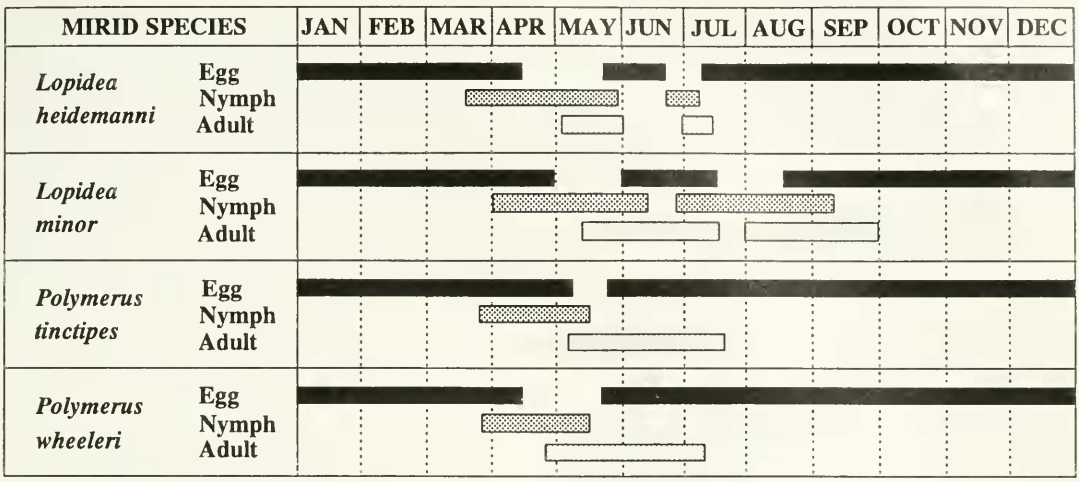


Fig. 4. Generalized mirid seasonal histories based on sampling of *Phlox subulata* in eastern West Virginia–southwestern Virginia, 1989–1994; see text for seasonality of populations occurring at higher altitudes and latitudes.

Cerastium arvense L.; adults were observed on *Quercus stellata* Wangenh.

Seasonal history and habits.—Overwintered eggs usually began to hatch from mid- or late March to early April in shale barrens of Virginia (Fig. 4) and mid- to late April in Pennsylvania serpentine barrens. In early season, the bright red nymphs were often shaken only from plants that were in bloom. Early instars fed on parts of the corolla, both in the field and laboratory, but probably also feed on the foliage. Although the needlelike leaves of *P. subulata* did not show feeding injury, chlorotic blotches were observed on the foliage of *V. villosa* fed on by *L. heidemanni* nymphs. In Virginia, fourth and fifth instars were present on *P. subulata* as early as mid- or late April (rarely in early April), with adults appearing during the first week of May (Fig. 4). Late-instar nymphs, however, were typically present in shale barrens until mid- or late May, often feeding on the fruits. Development of populations at the Kates Mountain shale barren (elevation about 760 m) lagged behind that in other barrens of Virginia and West Virginia (elev. generally 300–700 m). During 5–6 May 1990, for example, late instars and teneral adults were observed in several shale barrens of southwestern Virginia, but only third instars were seen on Kates Mountain.

First-generation adults of *L. heidemanni* often dispersed to nearby shrubs and trees soon after developing on *P. subulata*; adults were never as common on moss phlox as the nymphs. A short-distance dispersal from breeding hosts is known in several other *Lopidea* species (Asquith 1991). At several sites, a small second generation developed on *P. subulata*. The first through third instars observed in late June 1990 and fourth and fifth instars in late June 1994 apparently represented another generation rather than a late hatching of overwintered eggs. The collection of adults over a three-month period (19 May–18 August) in North Carolina (McPherson et al. 1983), and the appearance of adults in that state during April (A.G.W. unpublished data) is further evidence for bivoltinism in *L. heidemanni*. The latest records of adults on *P. subulata* were 10 July at the Head Waters shale barren in Virginia and 11 July at the West Virginia site near Slanesville. Adults, however, have been collected in West Virginia on other plants as late as 19 August (Wheeler et al. 1983).

On *P. nivalis* in North Carolina (Cabarrus

Co.), fourth instars were observed in mid-April 1990. During 19–23 April 1991, second and third instars were found on *P. bifida* in sand prairies of Illinois and on Boones Bluff at Camp Nelson, Kentucky, and fourth and fifth instars were present on *P. bifida* in Tennessee cedar glades.

Lopidea minor Knight

This widespread generalist feeder is found east of the Rocky Mountains to New York and south to Florida. A characteristic plant bug of the semiarid plains (Knight 1965), it occurs mainly in relict prairies, serpentine barrens, and shale barrens in the mid-Atlantic states. This plant bug was usually found on moss phlox growing in the most open, sunlit portions of shale barrens. Some of the records of *L. minor* have been published under names recently proposed as synonyms: *L. petalostemi* Knight, *L. johnstoni* Knight, and *L. phlogis* Knight (Asquith 1991).

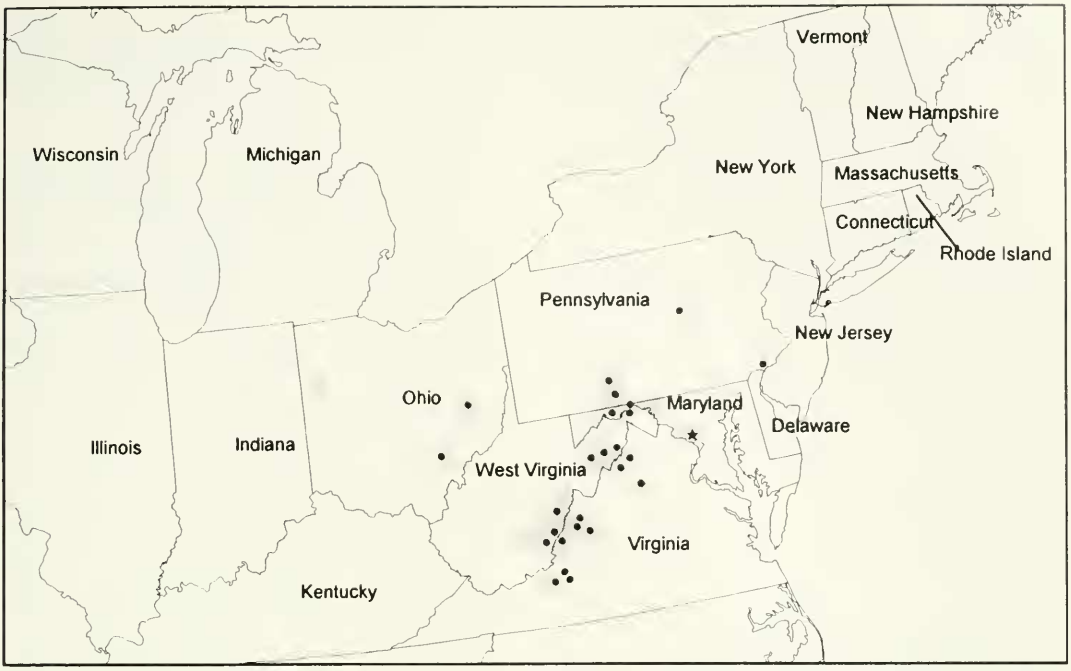
Distribution.—This orthotyline was described from Colorado and North Dakota (Knight 1918) and has since been recorded from Alberta, British Columbia, Florida, Illinois, Iowa, Kansas, Louisiana, Manitoba, Minnesota, Mississippi, Missouri, New York, North Carolina, Oklahoma, Pennsylvania, Saskatchewan, South Dakota, Texas, Virginia, West Virginia, and Wyoming (Henry and Wheeler 1988, Asquith 1991). Maryland is a new state record. *Lopidea minor* was present in 32 of 79 sites (Table 1).

Host plants.—In western North America, prairie clover (*Dalea purpurea* Vent var. *purpurea* (= *Pelalostemon purpureus*) serves as a common host (Knight 1927, 1941, 1965, Blinn and Yonke 1985); *L. minor* has also been recorded from the legume *Hedysarum* sp. in the Canadian Prairie Provinces (Kelton 1980). *Phlox subulata* is used as a host in the eastern United States (Knight 1965, Wheeler et al. 1983); records from this plant in a Pennsylvania serpentine barren and shale barrens in Virginia and West Virginia (Asquith 1991) were based on material collected during the present study.

In this study, *L. minor* was found only on *P. subulata* among the eastern narrow-leaved phloxes, occurring occasionally in ornamental plantings. Nymphs were also collected on *Eriogonum allenii, Paronychia montana* (Small) Pax & K. Hoffmann, and *Senecio anonymus* in shale barrens, and they were found once on and under a fern (*Cheilanthes lanosa* (Michx.) D.C. Eat.) in the Virginia shale barren near Eagle Rock in Botetourt Co. Adult males sometimes dispersed to flowers of *Chrysanthemum leucanthemum* L., *Sedum* spp., and grasses, and to fruits of *Staphylea trifolia* L.

Seasonal history and habits.—Hatching of overwintered eggs began in early or mid-April in shale barrens of southwestern Virginia and in late April in Pennsylvania serpentine barrens (Fig. 4). Egg hatch typically was spread over several weeks so that four or even all five nymphal stages overlapped in populations sampled during May. Nymphs are gray rather than bright red as in *L. heidemanni*. Adults first appeared in mid-May in more southern shale barrens, although late instars were often observed until early June; females persisted until mid-July. Each season, a clear-cut second generation was produced (Fig. 4), which confirms the bivoltine life history that had been suggested for *L. minor* (Asquith 1991). Egg hatch began in late June in southern shale barrens, and second-generation adults began to appear in late July. Late instars, however, were usually common through August and were sometimes present into September. The latest records of adults were 1–2 October in three Virginia shale barrens.

Nymphs of *L. minor,* while occasionally seen on flower buds of *Erigonum allenii* in shale barrens, were not observed on flower buds or inflorescences of *P. subulata.* They live within or under mats of moss phlox and apparently feed on leaves or stems. Second-generation nymphs develop in midsummer when moss phlox is essentially dormant,



Map 1. Known distribution of *Polymerus tinctipes*. Star = type locality; filled circles = new records (see also Table 1); shading = counties in which specimens were collected.

having finished blooming and produced seeds, and are restricted to feeding on foliage that often appears brownish rather than lush green as in April and May.

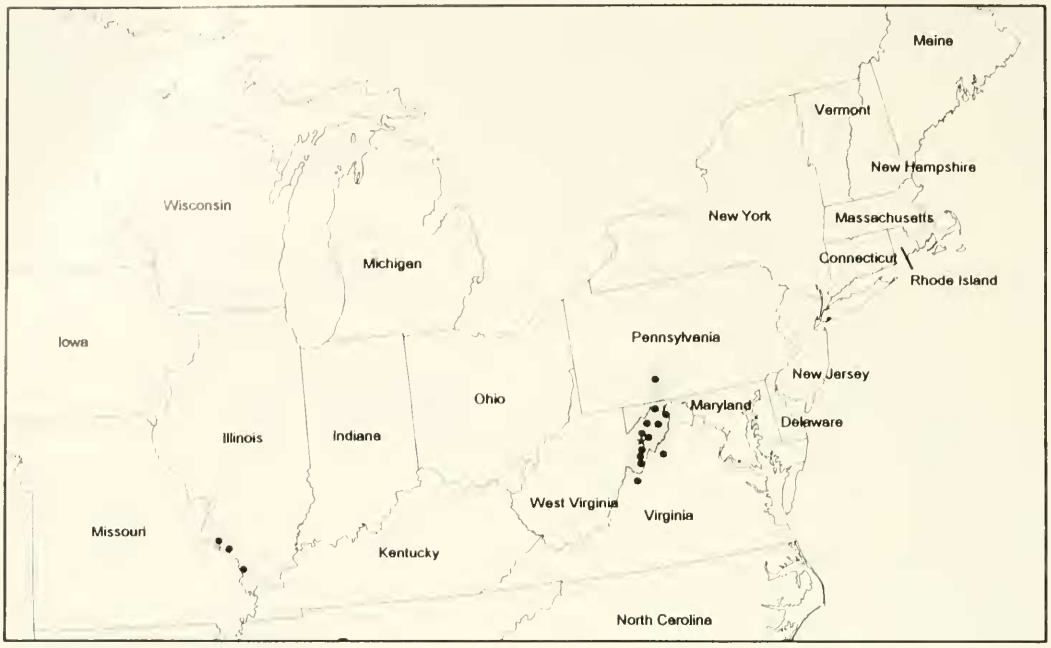
Polymerus tinctipes Knight

This phlox specialist has not been mentioned in the literature since its original description (Knight 1923), except in catalogs (Carvalho 1959, Henry and Wheeler 1988). It is, however, a characteristic species of moss phlox, the dearth of biological information merely reflecting entomologists' lack of attention to the insect fauna associated with this prostrate plant.

Distribution.—This mirine is known historically only from the type locality, Great Falls, Md., where four specimens were collected on 3 May 1915 (Knight 1923). In the present study, *P. tinctipes* was found on *P. subulata* at 32 of 79 sites sampled. New state records are Ohio, Pennsylvania, Virginia, and West Virginia (Map 1, Table 1).

Host plants.—No host has been previously recorded for *P. tinctipes,* the type specimens having been taken at Great Falls, Md., on a "lichen covered rock" (Knight 1923). This plant bug was found in the present study only on *P. subulata,* mainly in mid-Appalachian shale barrens and other shale outcrops, and in Pennsylvania serpentine barrens; it was also collected on moss phlox in a relict prairie in Ohio, a greenstone glade in the Blue Ridge of Virginia, and rarely in ornamental plantings. During visits to the type locality, where *P. subulata* grows on rocks above the Potomac River (Hitchcock and Standley 1919), this bug was found to be common. Adults mate on *P. subulata* and tend to remain on their host rather than disperse to nearby vegetation, unlike the two *Lopidea* species.

Seasonal history and habits.—Eggs of this univoltine mirid may hatch in late March, as evidenced by the presence of third instars during 8–12 April 1990. In most years,



Map 2. Known distribution of *Polymerus wheeleri*. Star = type locality; filled circles = new records (see also Table 1); shading = counties in which specimens were collected.

hatching probably does not begin in southwestern Virginia shale barrens until early or mid-April (Fig. 4). Eggs did not hatch until late April or early May in higher-elevation shale barrens (e.g. Kates Mountain) or sites at even higher latitudes, in serpentine barrens in Pennsylvania, and at sites in Ohio. Fourth and fifth instars were usually common in more southern shale barrens by early May. The green nymphs were observed to feed on flowers and fruits of *P. subulata*. The earliest record of adults was 7 May, but typically they did not appear until mid- to late May and were present only until late June or early July. The latest records for adults were 17–18 July at Millboro, Va., and Kates Mountain, W. Va.

Polymerus wheeleri Henry

The collection of this plant bug, at the time undescribed, from a West Virginia shale barren in 1978 was responsible for stimulating my interest in mirids and other insects associated with *P. subulata*. No additional collections of this phlox specialist have been reported since the original description (Henry 1979, Henry and Wheeler 1988).

Distribution.—This mirine has been known only from the type locality, a shale barren west of Petersburg, W. Va. (Henry 1979), which has nearly been destroyed by construction. New state records obtained during the present study are Illinois, Maryland, Pennsylvania, and Virginia (Table 1). *Polymerus wheeleri* was found at fewer sites (12 on *P. subulata*) than any of the other plant bugs associated with eastern narrow-leaved phloxes (Map 2, Table 1).

Host plants.—Described from specimens collected on *P. subulata*, this species is characteristic of the fauna of mid-Appalachian shale barrens and outcrops, as well as mats of *P. bifida* ssp. *bifida* that festoon limestone ledges and bluffs in the Ozark Division (Mohlenbrock 1986) of southern Illinois. It was not found on *P. subulata* in eastern serpentine barrens. *Polymerus wheeleri* adults

show little tendency to disperse to nearby plants, although at the Short Mountain shale barren in Virginia an adult was observed on flowers of the crucifer *Draba ramosissima.*

Seasonal history and habits.—Eggs of this univoltine, early-season species began to hatch at about the same time as those of *L. heidemanni*: generally late March to early April (Fig. 4). In 1991 the presence of a third-instar nymph (with firsts and seconds) at the Head Waters shale barren on 27 March suggests that hatching had begun by mid-March. Nymphs are dark red rather than green as in *P. tinctipes*; they fed on petals, sepals, fruits, and pedicels of *P. subulata,* but they may also feed on the foliage. Fourth instars were observed as early as 8 April but were not usually present until mid- to late April. Adults began to appear from late April to early or mid-May at most sites in Virginia and West Virginia, although in 1991 a fifth instar collected on 14 April at the Short Mountain shale barren molted just two days later when held at room temperature. Adults remained on mats of moss phlox and generally disappeared by late June, males usually dying 7–10 days before females. The latest records were 10–11 July at Head Waters, Va., and near Slanesville, W. Va.

Discussion

Phlox subulata supports an unexpectedly rich mirid fauna: two generalist and two specialist species. Many shrubs and trees of eastern North America do not serve as hosts for as many as four mirids (personal observation). Absent from the fauna of *P. subulata* and other eastern narrow-leaved phloxes of prostrate growth habit are mirids that develop on native and cultivated phloxes of erect growth; *Lopidea davisi* Knight (Cory and McConnell 1927) and *L. confluenta* (Say) (Asquith 1991, personal observation) were not encountered during this study.

Lopidea heidemanni, L. minor, Polymerus tinctipes, and *P. wheeleri* develop on the glandular *P. subulata* ssp. *brittonii* in the region sometimes referred to as the Southern Appalachian Highlands (Blauch 1975); they appear to be most common in the southern part of this region. These bugs were often present on *P. subulata* that colonized the most xeric sites. The importance of slope was evident when colonies subject to different exposures were sampled along a winding mountain road; mirids typically were found on moss phlox in the drier sites rather than in more mesic sites less than a kilometer away. Except for occasional individuals observed feeding on reproductive structures, the bugs generally were not seen on exposed portions of *P. subulata.* They perhaps remain mostly within or under mats of the host plant (at least by day) to reduce the risk of desiccation in shale barrens and other slopes of high insolation temperatures. Even when bugs were not apparent on host plants, several individuals (sometimes 5–10) could be found when a plant was shaken over a pan or tray.

Plant bugs that develop on *P. subulata* are characteristic members of a shale barren fauna, occurring in the Valley and Ridge Province on Upper Devonian shales of the Brallier formation (elev. 300–700 m) and on Ordovician Martinsburg outcrops in Virginia's Massanutten Mountains (elev. about 700 m at sample site). Only at the southern end of Short Mountain in the Massanutten complex, however, were all four mirid species observed at one site. *Polymerus tinctipes* was found at altitudes ranging from near sea level along the Potomac River at Great Falls, Md., to about 1040 m in Madison Co., Va., in the Blue Ridge. This species and the other mirids of *P. subulata* were generally scarce in the Blue Ridge (*Polymerus wheeleri* was absent).

Lopidea heidemanni, which shows the greatest diet breadth among the four species, occurred on *P. subulata* at more sites (62) than any of the other plant bugs and was the sole mirid recorded from 19 sites. It was also found in several ornamental plantings of *P. subulata* and developed on

P. bifida and *P. nivalis,* the other eastern narrow-leaved phloxes. It was the only one of the four mirid species that developed on *P. divaricata* among the phloxes of upright growth habit that were sampled in the Appalachians during this study.

The generalist *L. minor* and phlox specialist *P. tinctipes* were both found at 32 sites and showed spotty distributions in shale and in serpentine barrens; they coexisted at 12 sites. Both were found occasionally in landscape colonies of *P. subulata.* Their presence perhaps was the result of being moved with native plants collected for ornamental use, or possibly should be attributed to dispersal to ornamental plants from nearby native colonies of *P. subulata.* The surprising record of *P. tinctipes* from an ornamental planting in Northumberland Co., Pa. (E. of Milton), might be explained by this site's proximity to the historical occurrence of the host 1.5 mi. ESE of Milton (1961 record in herbarium of Academy of Natural Sciences, Philadelphia).

The specialist *P. wheeleri* occurred at 12 sites in shale barrens and outcrops, coexisting with *P. tinctipes* at only 2 sites; it was absent from serpentine barrens. It also developed on *P. bifida* in the Ozark region of southern Illinois. Another phlox specialist, the psyllid *Craspedolepta eas,* shows a similar disjunct distribution (Wheeler 1994). Appalachian-Ozarkian distributions are also known in other insect groups (e.g. Ross 1944, Stannard 1968, Pratt et al. 1994), and the two regions have long been considered "faunally related" (e.g. Holt 1969).

Mirids were nearly always present and, often, were abundant in colonies of *P. subulata* in eastern West Virginia and western Virginia, an area that likely is the host plant's dispersal center (Wherry 1935b). Plant bugs typically were scarce or absent from *P. subulata* colonies in northern New Jersey and Pennsylvania and in New York, but more sampling is needed to determine if the *Polymerus* spp. might be present in these formerly glaciated areas. Additional sampling is also necessary to determine if mirids are associated with *P. subulata* on Bluff Mountain (Tucker 1972), which is near the fringe of this plant's range in northwestern North Carolina.

The Southern Appalachian Highlands is a center of distribution for *P. tinctipes* and *P. wheeleri,* species that can be considered monophagous (i.e. restricted to developing on *Phlox* spp.). How these specialists on mat-forming phloxes came to occupy this region and their history during the Pleistocene remain unknown. *Polymerus tinctipes* may prove to be a southern Appalachian endemic.

The two *Polymerus* species represent the most significant discoveries among the mirids that occur on eastern narrow-leaved phloxes. *Polymerus tinctipes* had been known previously only from the type locality and its host had remained unrecorded; *P. wheeleri* was an undescribed species whose collection prompted a closer look at mirid-phlox associations in shale barrens. The distribution of both specialist herbivores is now better known, and information on their host plant range and seasonality is available. Much, however, remains to be learned about their distribution and habits; a phylogenetic study of the genus would elucidate the relationship of these apparently closely related species and, perhaps, suggest modes of speciation.

Lopidea minor and *Polymerus tinctipes* can be considered characteristic insects of serpentine barrens. In addition, these species, plus *P. wheeleri,* are as characteristic of shale barrens as the much better known endemic plants occurring in these communities. The plant bugs are subject to the same types of anthropogenic disturbances (road construction, quarrying, etc.) that threaten the shale (and serpentine) barren flora. Protection of Appalachian shale barrens will not only preserve the endemic plants of these communities but also the phytophagous insects that depend on them. This specialized biota can be used in studies

of island biogeography (see Tepedino and Stanton 1976) and eventually may be useful in helping to interpret the complex history of the Appalachians.

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